POLLEN MORPHOLOGY AND CLASSIFICATION OF THE PYROLACEAE AND MONOTROPACEAE[1]

BY JOAN W. NOWICKE[2]
Department of Botany, Washington University and
Missouri Botanical Garden, St. Louis.

ABSTRACT

Pollen morphology of the *Pyrolaceae* and *Monotropaceae* reinforces the view that the *Pyrolaceae* and *Ericaceae* are closely related and that the *Monotropaceae* should be treated as a distinct family. It further supports the separation of *Moneses uniflora* and *Orthilia secunda* from the genus *Pyrola,* and in the *Monotropaceae* it suggests a realignment of species within the *Hypopitys-Monotropa* complex.

The *Pyrolaceae* as aligned by Schultze-Motel (1964) constitute a diverse group consisting of two subfamilies *Pyroloideae* and *Monotropoideae,* the latter largely saprophytic. Others have reduced one or both taxa to subdivisions of the *Ericaceae,* either as the tribe *Pyroleae* (Bentham & Hooker, 1873), or as the subf. *Monotropoideae* with the *Pyroleae* included in the subf. *Arbutoideae* (Copeland, 1941, 1947). A palynological study was made to determine if pollen morphology, a relatively unused attribute, might better characterize the affinities of the taxa involved.

Erdtman (1952), largely following the systematic treatment of Drude (1889), described the pollen of 15 species representing eight genera. According to him, species of *Pyrola* L. have pollen united in tetrads with individual grains 3-colporate; pollen of *Chimaphila umbellata* Nutt. is in tetrads with apertures not always sharply delimited; pollen of *Moneses uniflora* (L.) Gray also is united in tetrads in which individual grains are 3-colp(oroid)ate; and *Ramischia secunda* (L.) Garcke [=*Orthilia secunda* (L.) House] has single grains which are (2-) 3-colporate. In the *Monotropoideae,* Erdtman described pollen of *Monotropa hypophegea* Wallr. as (2-) 3-colporate, *Pleuricospora fimbriolata* Gray as (3-) 4-colporoidate, *Pterospora andromedea* Nutt. as 4 (-5)-colporoidate, and *Sarcodes sanguinea* Torrey as 4 (-5)-colpate. Erdtman utilized Copeland's (1938) description of *Allotropa virgata* Torrey & Gray which was noted as three-grooved.

Copeland (1934, 1935, 1937, 1938, 1939, 1941, 1947), in an extensive anatomical and systematic study of the tribe *Pyroleae* and subf. *Monotropoideae,* included a brief description of pollen of various genera. In his treatment of the *Pyroleae* (1947), he recognized four genera with the pollen grains of *Ramischia* Opiz (=*Orthilia* Raf.) solitary and tricolpate, those of *Chimaphila* Pursh in easily disrupted tetrads, those of *Pyrola* united in tetrads with the wall of each individual grain "marked by three half-grooves, continued as half grooves on the three as-

---

[1] Supported by Grant No. GB-3825 from the National Science Foundation issued to Dr. Walter H. Lewis.

[2] I wish to thank the curators of the herbaria (MO, F) for the use of herbarium specimens and for the extraction of pollen.

sociated grains," and grains of *Moneses* Salisb., which Copeland thought tenable as a district genus, also in tetrads.

In his summary article on the *Monotropoideae*, Copeland (1941) divided the group into four, or tentatively five, tribes. The most primitive tribe, *Pterosporeae*, consists of three monotypic genera, viz. *Pterospora* Nutt. with four-grooved pollen (1941), *Sarcodes* Torrey characterized by four-grooved pollen (1941), and *Allotropa* Torrey & Gray with three-grooved pollen (1938). The *Pleuricosporeae*, with only *Pleuricospora* Gray, have four-grooved pollen (1937). The largest tribe, *Monotropeae*, includes: *Monotropsis* Schweinitz in which Copeland (1939) recognized three species having pollen with "a thin exine, smooth except for two grooves lying in the same great circle;" *Hypopitys* Hill which Copeland (1941) believed monotypic [including all five of Small's (1914) species] with two-grooved pollen; *Pityopus* Small described by Copeland (1935) as having solitary grains with smooth walls and germinating through two opposite pores; *Monotropa* L., "apparently monotypic," consisting only of *M. uniflora* L. (Copeland, 1941) and characterized by three-grooved pollen; and two remaining genera, *Monotropastrum* Andres and *Wirtgenia* Andres, were not described. The last tribe, *Hemitomeae*, consists solely of *Hemitomes* Gray, having two-grooved pollen (1941). According to Copeland (1941) possibly a fifth tribe in the subf. *Monotropoideae* should be recognized for the unplaced Oriental genus *Cheilotheca* Hook f.

On a regional basis Erdtman et al. (1961) described the pollen of Scandinavian representatives of the *Ericales*, and Oldfield (1959) characterized the pollen of western European members of this order.

Twelve genera representing 31 species have been examined palynologically. Mature buds, or anthers only, were removed from herbarium specimens and acetolyzed according to the procedure outlined in Erdtman (1952). A complete set of slides is maintained at Missouri Botanical Garden Herbarium with vouchers at either the Missouri Botanical Garden Herbarium (MO) or the Field Museum of Natural History, Chicago (F).

In this survey no attempt is made to revise the species studied, for except as noted the species within each genus are similar palynologically. The specific names used largely follow treatments in the latest floras available.

PYROLACEAE

Pyrola L. (11 species of 40±)

All species examined were essentially similar in pollen morphology. Pollen of *Pyrola secunda* L., treated here as *Orthilia secunda* (L.) House, differs from all species of *Pyrola*.

Grains in tetrads, ca 31μ in diam, individual grains 3-colporate, total adjacent colpi length ca 15.5μ, exine ca 1.7μ in thickness, sexine ± equal to nexine and coarsely reticulated.

Pyrola americana Sweet, *Anderson & Peck s.n.* (MO), Michigan; *P. angustifolia* (Alef.) Hemsl., *Hinton s.n.* (MO), Mexico; *P. aphylla* Smith, *Butler 1575* (MO), California; *P. asarifolia Michx., Heacock 146* (MO), British Columbia;

P. chlorantha Swartz, *Sewell & Weed s.n.* (MO), Labrador; *P. grandiflora* Radius, *Ekblow 591* (MO), Greenland; *P. media* Sw., *Ahlberg s.n.* (MO), "Scandinavia"; *P. minor* L., *Hitchcock & Muhlick 13147* (MO), Montana; *P. rotundiflora* L., *Holm s.n.* (MO), D. C.; *P. sparsifolia Suksdorf, Suksdorf 2695* (MO), Washington; *P. uliginosa* Torrey & Gray, *Cronquist 1744* (MO), Idaho.

Moneses Salisb. (monotypic)

Grains in tetrads, ca 31μ in diam, individual grains 3-colpate, colpi ca 8μ in length, exine ca 2μ in thickness, sexine somewhat thicker than nexine and finely reticulated.

Moneses uniflora (L.) Gray, *Palmer* 37563 (MO), S. Dakota.

Orthilia Raf. (monotypic)

Grains single, subprolate, ca 20μ(E) × 15.5μ(P), 3-colporate, colpi ca 13μ in length, ora ca 1.3μ in diam, exine ca 1μ in thickness, sexine ± equal to nexine and finely reticulated.

Orthilia secunda (L.) House, *Thompson & Thompson 601* (F), British Columbia (as *Pyrola secunda* L.)

Chimaphila Pursh (3 species of 4±)

Grains in tetrads (with tetrads tending to clump together after acetolysis), ca 39μ in diam (ca 36μ for *C. umbellata*), individual grains 3-colpate, colpi irregular and vague, exine ca 2μ in thickness (varying from 2.0-2.5μ in *C. occidentalis*), sexine ± equal to nexine and finely reticulated.

Chimaphila maculata (L.) Pursh, *Churchill s.n.* (MO), New Jersey; *C. occidentalis* Rydb., *Mason 7452* (MO), Washington; *C. umbellata* Nutt., *Henderson 5589* (MO), Oregon.

MONOTROPACEAE

Allotropa Torrey & Gray (monotypic)

Grains single, subprolate, ca 23μ × 20μ, 3-colporoidate, colpi ca 13μ in length, ora small, ca 2.5μ in diam, exine ca 1.3μ in thickness, sexine ± equal to nexine and finely reticulated.

Allotropa virgata Torrey & Gray, *Meyer 1120* (MO), Washington.

Pterospora Nutt. (monotypic)

Grains single, prolate spheroidal, ca 22μ × 20μ, 3- to 4-colporoidate, colpi ca 13μ in length, ora narrow and vague (Fig. 1), exine ca 1.8μ in thickness, sexine ± equal to nexine and finely reticulated.

Pterospora andromedea Nutt., *Churchill s.n.* (MO), Michigan.

Sarcodes Torrey (monotypic)

Grains single, ± spheroidal, ca 30μ in diam, 3- to (4-) colp(oroid)ate, colpi ca 11μ in length, ora as one or two weak areas near extremes of colpi (Fig. 2), exine ca 1.8μ in thickness, sexine somewhat thicker than nexine and finely reticulated.

Sarcodes sanguinea Torrey, *Parish* 3466 (MO), California.

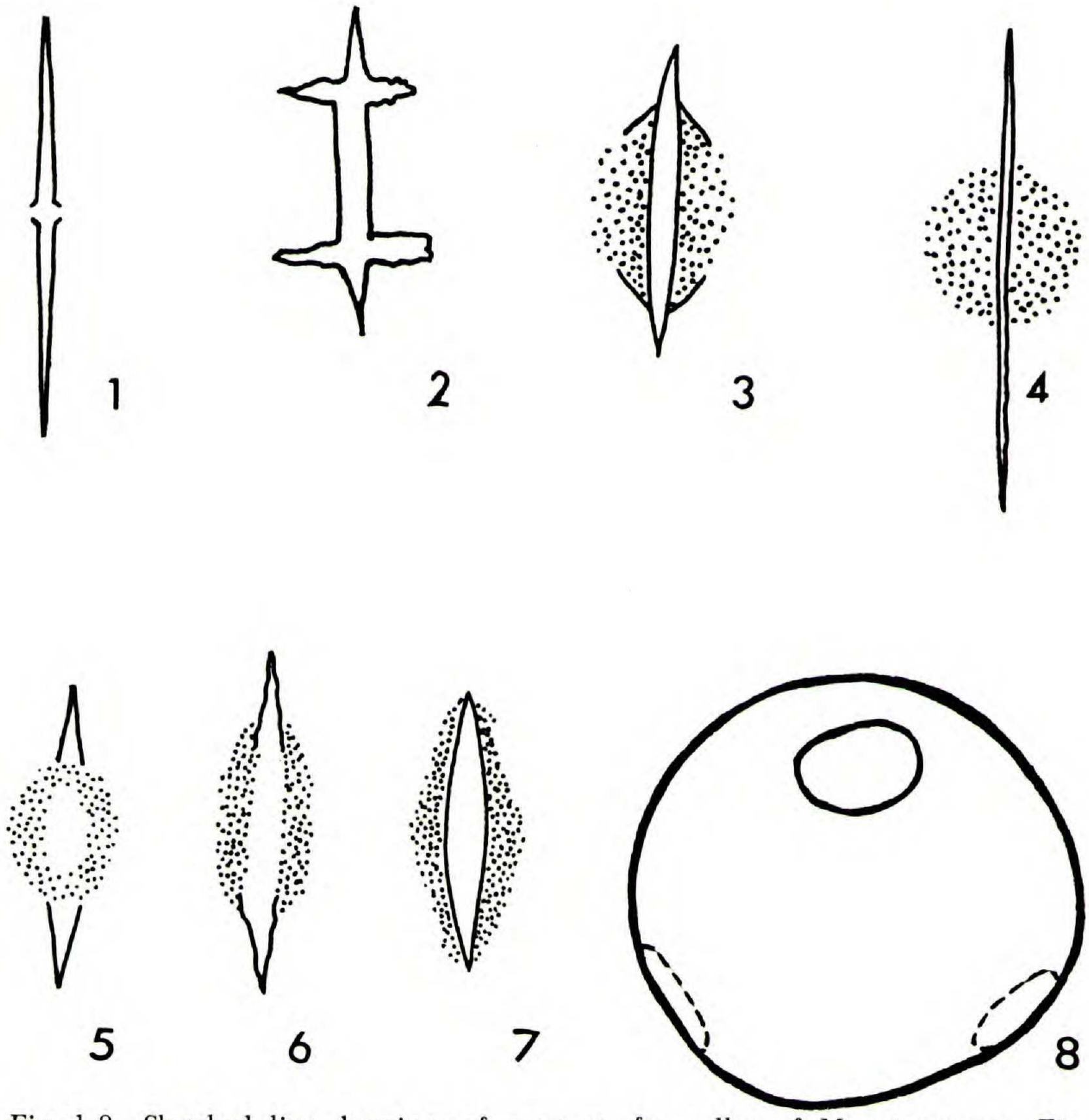

Fig. 1-8. Sketched line drawings of apertures for pollen of *Monotropaceae*. Fig. 1-7, ×3000; Fig. 8, ×1500. Fig. 1. *Pterospora andromedea*. Fig. 2. *Sarcodes sanguinea*. Fig. 3. *Pleuricospora fimbriolata*. Fig. 4. *Monotropsis odorata*. Fig. 5. *Hypopitys monotropa*. Fig. 6. *H. lanuginosa*. Fig. 7. *H. latisquama*. Fig. 8. *Monotropa uniflora* (entire grain).

Pleuricospora Gray (monotypic)

Grains single, ± spheroidal, ca 26μ in diam, (-4) to 5-colporate, colpi ca 10μ in length, ora ca 6μ in length and laterally vague (Fig. 3), exine ca 2μ in thickness, sexine ± equal to nexine and essentially smooth.

Pleuricospora fimbriolata Gray, *Cooke 16129* (MO), California.

Hemitomes Gray (monotypic)

Grains single, prolate spheroidal, ca 28μ × 27μ, (2-) to 3-colporate, colpi ca 14μ in length, ora ca 6.5μ in diam, exine ca 1.5μ in thickness, sexine somewhat thinner than nexine and finely reticulated.

Hemitomes congestum Gray, *Meyer 654* (MO), Washington [as *Newberrya congesta* (Gray) Torrey].

Monotropsis Schweinitz (2 species of 3±)

Grains single, prolate spheroidal, ca 26μ × 24.5μ, 2-colporate, colpi ca 15μ in length, ora ca 5.2μ(length) × 6.5μ(width) as in Fig. 4, exine ca 2μ in thickness, sexine ± equal to nexine and very finely reticulated.

Monotropsis odorata Ell., *Plitt s.n.* (MO), Maryland; *M. reynoldsiae* (Gray) Heller, *Reynolds s.n.* (F), Florida (as *Schweinitzia reynoldsiae* Gray).

Hypopitys Hill (6 species)

H. americana (DC.) Small. Grains single, prolate spheroidal, ca 21μ × 20μ, 2-colporate, colpi ca 12μ in length, ora ca 9μ × 6μ, exine ca 2μ in thickness, sexine ± equal to nexine and finely reticulated.

H. hypophegea (Wallr.) G. Don. Grains single, subprolate, ca 18μ × 21μ, 2- to (3-) colporate, ora irregular in shape but ± equal in length to colpi, exine ca 1.3μ in thickness, sexine almost smooth.

H. lanuginosa (Michx.) Raf. Grains single, ± spheroidal, ca 21μ in diam, 2-colporate, colpi ca 11μ in length, ora ca 6μ × 4μ (Fig. 6), exine ca 1.5μ in thickness, sexine somewhat thicker than nexine and finely reticulated.

H. latisquama Rydb. Grains single, prolate spheroidal, ca 23μ × 22μ, 2- to (3-) colporate, colpi ca 9μ in length, ora ca 8μ × 5μ (Fig. 7), exine ca 1.5μ in thickness, sexine ± equal to nexine and finely reticulated.

H. monotropa Crantz. Grains single, prolate spheroidal, ca 24μ × 22μ, 2- to (3-) colporate, colpi ca 9μ in length, ora ca 4μ in diam (Fig. 5), exine ca 1.3μ in thickness, sexine very finely reticulated.

H. sanguinea Heller. Grains single, flattened on four sides or ± spheroidal, ca 21μ in diam, 2-colporate, colpi ca 11μ in length, ora ca 8μ × 5.5μ, exine variable in thickness from 1.3-2.0μ, sexine ± equal to nexine and finely reticulated.

Hypopitys americana (DC.) Small, *Duncan 9931* (MO), Georgia; *H. hypophegea* (Wallr.) G. Don, *Santesson 14801* (F), Sweden (as *Monotropa hypophegea* Wallr.); *H. lanuginosa* (Michx.) Raf., *Applegate* 3855 (F), California (as *Monotropa lanuginosa* Michx.); *H. latisquama* Rydb., *Meyer 1011* (MO), Washington; *H. monotropa* Crantz, *Holmgrew 1268* (F), Sweden (as *Monotropa hypopitys* L.); *H. sanguinea* Heller, *Blumer s.n.* (MO), Arizona.

Monotropa L. (2 species)

M. coccinea Zucc.. Grains single, oblate spheroidal, ca 27μ × 30μ, 3-porate, ora ca 5.5μ in diam, exine less than 1μ, sexine smooth.

M. uniflora L. Grains single, suboblate, ca 24μ × 28μ, 3-porate, ora ca 6μ × 8μ (Fig. 8), exine less than 1μ, sexine smooth.

The above have been considered as one by several authors (Andres, 1910; Domin, 1915), but minor differences in pollen morphology suggest that they may be distinct.

Monotropa coccinea Zucc., *Johnson* 777 (F), Guatemala; *M. uniflora* L., *Gillett & Findlay* 5469 (MO), Labrador.

Discussion

The status of the *Pyrolaceae* and *Monotropaceae* in relation to the *Ericaceae* and to one another has been a matter of some conjecture. In earlier judgements palynological data have never been fully utilized. The *Pyrolaceae*, with the single exception of *Orthilia secunda*, have grains united in tetrads, mostly 3-colporate with small ora in contrast to the single grains and graded variations of compound and porate apertures observed in the *Monotropaceae*. Such differences reinforce the

treatment in recent floras (Bish, 1952; Bobrov, 1952; Moss, 1959; Clapham et al., 1962) where at least the *Monotropaceae* are considered distinct from the *Pyrolaceae*. For the same reasons the family should also be distinguished from the *Ericaceae*. On the other hand there may be validity in placing the *Pyrolaceae* in the *Ericaceae*, since in an earlier study of more than 250 ericaceous species, I found that the pollen from both taxa were, almost without exception, strikingly similar wih grains united in tetrads and individually 3-colporate. Wodehouse (1932), in examining pollen of a new genus in a related family, the *Clethraceae*, also briefly noted that the *Pyrolaceae* are unquestionably ericaceous. Many authors relegate the taxon to subfamilial or even tribal status under the *Ericaceae* (Bentham & Hooker, 1873; Copeland, 1947; Hitchcock et al., 1959) and my pollen data would support this treatment.

Within the "*Pyrolaceae*" most of the species in each genus are almost identical in pollen morphology. Two exceptions occur in species formerly placed with *Pyrola*. *Moneses uniflora*, thought by Copeland (1947) to be tenable as a distinct genus, has pollen united in tetrads like most members of the "family", but is atypical in *Pyrola* for the grains lack an os and are only 3-colpate. Considering the conservative pollen morphology of most species of *Pyrola*, this divergence could well represent a character significant at the level of genus. *Orthilia secunda* is the only species to have single grains; it should also be set apart from *Pyrola* in agreement with House (1921).

In the *Monotropaceae*, although a wide range of aperture types is represented, there exists a graded sequence in the variation present. The *Pterosporeae* were considered by Copeland (1941) as the most primitive tribe, and their pollen morphology, mostly 3-colporoidate, reinforces this view. *Sarcodes*, with its ora usually represented by two weak areas near the extremes of the colpus, a condition accentuated by acetolysis also present to a lesser degree in grains treated only with 2% acetic-orcein, may represent an evolved palynological condition though otherwise resembling *Allotropa* and *Pterospora*.

With the exception of *Monotropa*, the remaining genera studied, *Pleuricospora*, *Hemitomes*, *Monotropsis*, and *Hypopitys*, possess pollen with a second type of aperture. This is colporate in which the extent of the os and the sharpness of its delimitation, as well as aperture number, parallel somewhat the established generic alignments. *Pleuricospora*, although considered advanced in the number of apertures, has nevertheless, an os which because of its lateral vagueness, may mark the most primitive genus in respect to pollen morphology. *Hemitomes* and *Monotropsis*, while differing somewhat in their colpus length, have a more or less circular os which is well delimited.

Within those species grouped in *Monotropa* (Moss, 1959; Clapham et al., 1962; Schultze-Motel, 1964) the morphology of the pollen represents two highly divergent forms. The pollen of the one group, including the type of *Hypopitys*, *H. monotropa* Crantz, is 3-colporate and mostly prolate spheroidal, whereas the pollen of the second group, including the type of *Monotropa*, *M. uniflora* L., is 3-porate and oblate spheroidal or suboblate. This agrees with Copeland's (1941) separation of

the genera. However, he concluded that both were monotypic but, even from the examination of pollen alone, differences between species of *Hypopitys* (Fig. 5, 6, 7) and between *M. uniflora* and *M. coccinea* are noteworthy, and for the present are considered as separate species.

Palynologically *Monotropa* is the most distinct member of the *Monotropaceae* (Fig. 8) and probably the most highly evolved. It is the only representative of the third pollen type, 3-porate, otherwise rare in the *Ericales*.

Literature Cited

Andres H. 1910. Die *Pirolaceae* des Aschersonschen Herbariums. Bot. Verein Prov. Brandenberg **52:** 90-95.

Bentham, G. and J. D. Hooker. 1873. *Ericaceae* & *Monotropeae*, p. 577-608, Genera Plantarum **2.**

Bish, N. A. 1952. *Pyrolaceae*, p. 7-19, *In* Flora of U.S.S.R. Vol. **18.**

Bobrov, E. G. 1952. *Monotropaceae*, p. 19-22, *In* Flora of U.S.S.R. Vol. **18.**

Clapham, A. R., T. G. Tutin & E. F. Warburg. 1962. Flora of the British Isles. Cambridge University Press.

Copeland, H. F. 1934. The structure of the flower of *Newberrya*. Madroño **2:** 137-142.

———. 1935. On the genus *Pityopus*. loc. cit. **3:** 154-168.

———. 1937. The reproductive structures of *Pleuricospora* loc. cit. **4:** 1-16.

———. 1938. The structure of *Allotropa*. loc. cit. 137-153.

———. 1939. The structure of *Monotropsis* and the classification of the *Monotropoideae*. loc. cit. **5:** 105-118.

———. 1941. Further studies on *Monotropoideae*. loc. cit. **6:** 97-119.

———. 1947. Observations on the structure and classification of the *Pyroleae*. loc. cit. **9:** 65-102.

Domin, K. 1915. Vergleichende Studien uber den Fichtenspargel. Sitzungsb. kgl. bohm. Ges. Wiss. Prag., II Kl., I Stück: 1-111.

Drude, O. 1889. *Pirolaceae*, *In* Engler & Prantl, Nat. Pflanzenf. IV. **1:** 3-11.

Erdtman, G. 1952. Pollen morphology and plant taxonomy. Angiosperms. Almqvist & Wiksell, Stockholm.

———, B. Berglund & J. Praglowski. 1961. An introduction to a Scandinavian pollen flora. Almqvist & Wiksell, Stockholm.

Hitchcock, C. L., A. Cronquist, M. Ownbey, & J. W. Thompson. 1959. Vascular plants of the Pacific Northwest. Part 4. Univ. of Washington Press, Seattle.

House, H. D. 1921. Nomenclatorial notes on certain American plants. I. Amer. Midl. Nat. **7:** 126-135.

Moss, E. H. 1959. Flora of Alberta. Univ. of Toronto Press, Toronto.

Oldfield, F. 1959. The pollen morphology of some of the West European *Ericales*. Pollen et Spores **1:** 19-48.

Schultze-Motel, W. 1964. *Pyrolaceae*, p. 381-383, *In* Engler, Syllabus der Pflanzenf. **2.** Gebrüder Borntraeger, Berlin.

Small, J. K. 1914. *Monotropaceae*, p. 11-18, *In* North American Flora. Vol. **29.**

Wodehouse, P. G. 1932. *In* Smith & Standley, *Schizocardia*, a new genus of trees of the family *Clethraceae*. Trop. Woods **32:** 8-11.